

PLANT SPECIATION ASSOCIATED WITH GRANITE OUTCROP COMMUNITIES OF THE SOUTHEASTERN PIEDMONT¹

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Granite outcrop communities of the southeastern Piedmont have long been of interest to the systematic botanist because of their large assemblage of endemic taxa. Crystalline rock exposures, called "flat-rocks" or "granite outcrops," occur sporadically from North Carolina to Alabama, and their combined extent is estimated to be about 12,000 acres. Ten of the best-documented species reported to be

ENDEMIC SPECIES	Table 1. GEOGRAPHIC ZONES (FIG. 1)					
	10	9	8	7	6	3
<i>Isoetes melanospora</i>	×					
<i>Rhynchospora saxicola</i>	×	×				
<i>Viguiera porteri</i>	×	×	×			
<i>Quercus georgiana</i>	×	×	×	×		
<i>Amphianthus pusillus</i>	×	×	×	×	×	
<i>Phacelia maculata</i>	×	×	×	×	×	
<i>Sedum pusillum</i>	×	×	×	×	×	
<i>Portulaca smallii</i>	×	×	×	×	×	×
<i>Cyperus granitophilus</i>	×	×	×	×	×	×
<i>Juncus georgianus</i>	×	×	×	×	×	×

Occurrence of 10 plant species endemic to granite outcrop communities in the Piedmont of southeastern United States.

enedmic to granite outcrop communities are listed in Table 1. When their collective ranges are plotted on a single map, all ten species are found to occur within a small region of the upper Piedmont of Georgia, east of Atlanta (the innermost circle of Fig. 1). Toward the southwest and northeast the number of endemic taxa gradually decreases until only three of the species listed in Table 1 are found to be associated with granite outcrops in eastern North Carolina. This "center of endemism" in Georgia is coincident with the geographic center of the greatest concentration of exposed rock.

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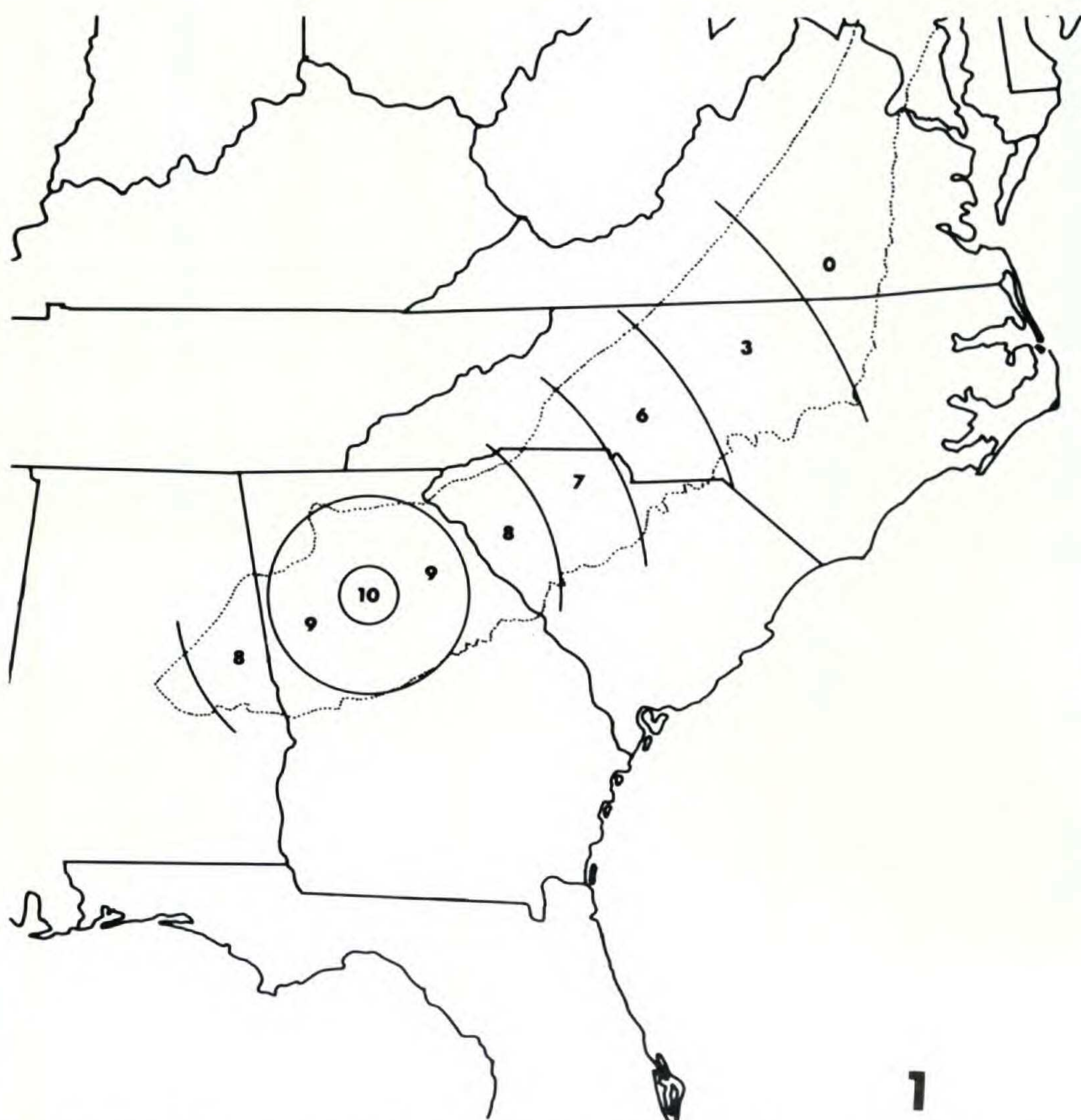


Fig. 1. Diagram to show how the number of species of granite outcrop endemics listed in Table 1 diminishes along a northeast-southwest axis from a "center of endemism" located in the central Piedmont of Georgia. The number of species is also taken as the number for the geographic zone (Table 1).

A variety of habitats are afforded by the granite outcrops. Two of the most important types available to higher plants are: 1) depression pits in the rock surface, which can be classified into a number of different community types by the correlates of soil depth and vegetation cover (Burbank and Platt 1964); and 2) glade-like, border areas of thin soil situated between rock exposures or between rock and adjacent forest or field.

The granite outcrops have been open to plant habitation for a long period of time although the longevity of any single exposure may not be great. Sufficient time has elapsed, for example, for the rare endemic *Amphianthus pusillus* Torr. to become adapted to an exceedingly specialized and infrequent habitat. It presently occupies depression pits of a critical size, topography, soil depth, and water retentive capacity. Furthermore, it has had time to diverge from close relatives to the extent that it now constitutes a monotypic genus of uncertain taxonomic affinities. Pennell (1935), in his monograph of the Scrophulariaceae, notes that the *Amphianthus* habit of bearing flowers both on elongated floating stems and also at the base of the plant, where they are immersed and cleistogamous, has no counterpart among the Scrophulariaceae.

The strikingly high degree of endemism associated with the outcrops suggests that they have long served as active sites for speciation in the southeast. A few of the endemic species may be remnants of once more widespread species which had their origin elsewhere. However, most endemic taxa appear to have had their origin in adaptation to outcrop habitats; most by gradual, ecogeographical processes and perhaps a few by an abrupt, saltation process. The Piedmont Region marks the geographic limit of distribution for many Coastal Plain and Appalachian species and the granite outcrops provide a variety of ecologically-marginal habitats to which geographically-peripheral populations may adapt.

The processes associated with speciation may actually undergo acceleration in the region of granite outcrops. Outcrops frequently occur in clusters with exposures separated by a few miles or less, and the clusters, in turn, separated from one another by greater distances. Species characteristic of, or endemic to, outcrop communities are consequently subdivided into a number of disjunct populations. Thus, semi-isolated populations are able to diverge from nearby populations as well as occasionally cross with them. Wright (1931) considered this type of population to be capable of rapid evolution.

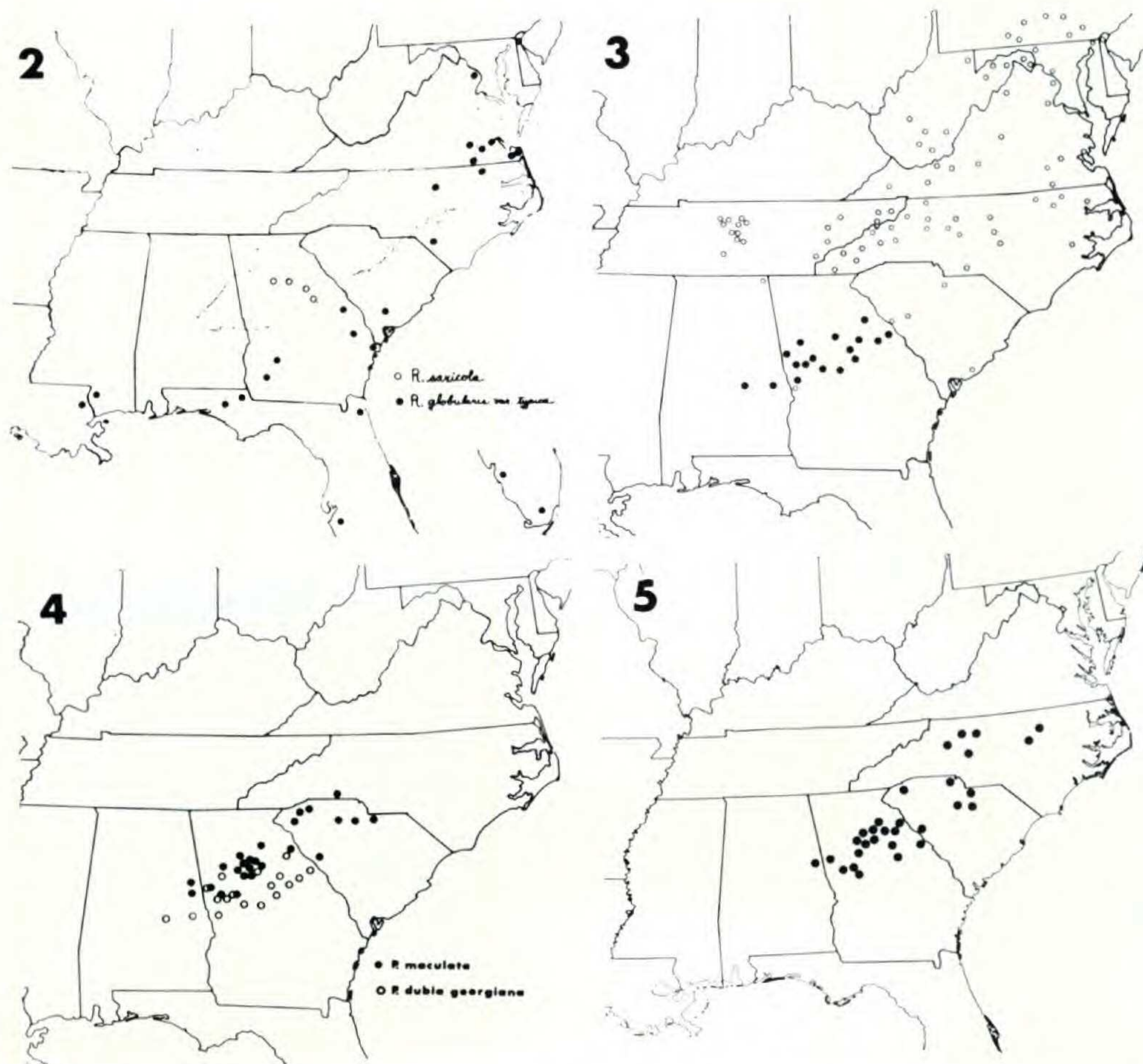


Fig. 2-5. Distribution maps. Fig. 2, *Rhynchospora saxicola* and *R. globularis* var. *typica*. Fig. 3, *Phacelia dubia* (open circles) and *P. dubia* var. *georgiana* (solid black circles). Fig. 4, *Phacelia maculata* and *P. dubia* var. *georgiana*. Fig. 5, *Cyperus granitophilus*.

ECOGEOGRAPHICAL SPECIATION

The fact that several endemic species are situated at the geographic periphery of their nearest relative is taken as indirect evidence of past ecogeographical speciation in association with granite outcrop communities. For example, *Rhynchospora saxicola* Small and *Portulaca smallii* P. Wilson occur at the boundary of the ranges of their putative, Coastal Plain progenitors, *R. globularis* var. *typica* (Gale 1944), as illustrated in Fig. 2, and *P. pilosa* (Wilson 1932, Steiner 1944, Cotter and Platt 1958) respectively. These taxa are in need of modern systematic treatment in order to more accurately assess their specific status and

evolutionary history. Another endemic species, *Phacelia maculata* Wood, which will be discussed below, is presently distributed at the southeastern boundary of the range of its closest relative, *P. dubia* of the Appalachians.

Recent ecogeographical speciation is indicated by the number of sub-specific taxa endemic to the outcrops. The systematics of one of these, *Phacelia dubia* var. *georgiana*, has been described in a recent report (Murdy, 1966). This variety was named by McVaugh (1943) as a race of *P. dubia* which could be distinguished from the latter on the basis of leaf characters. Constance (1949), in his revision of *Phacelia* species in the subgenus *Cosmanthus*, referred to it as a distinct regional phase of the Appalachian *P. dubia* restricted to granite rocks in the Piedmont of Alabama and Georgia (Fig. 3).

Population studies have revealed that the ecotype *P. dubia* var. *georgiana* can be separated from the main body of the species on the basis of any one of a number of quantitative traits, such as length of calyx, petals, and sepal hairs. The ecotype has the same chromosome number as *P. dubia* ($n = 5$) and artificial crosses between them have produced vigorous hybrids. The ecotype occurs in abundance on outcrops of the lower Piedmont (Fig. 3), and in this region, it has become an integral component of communities both in depression pits and in border areas. Its origin appears to have been recent and in the lower Piedmont. It has not yet migrated to the "center of endemism," in the upper Piedmont of Georgia, where a niche appears to be open to it.

Phacelia maculata is a species endemic to granite outcrops of the upper Piedmont from North Carolina to Alabama (Fig. 4). It is a poor competitor when compared with *P. dubia* var. *georgiana* and when both occur at the same outcrop site, the former is largely confined to deciduous glades bordering the exposed rocks, whereas *P. dubia* var. *georgiana* occupies a variety of open habitats. All of the systematic data to date suggests that *P. maculata* and *P. dubia* formerly diverged from a common, 5-chromosome

stock. Today, they are reproductively isolated by means of a postfertilization, incompatibility factor (Murdy 1966).

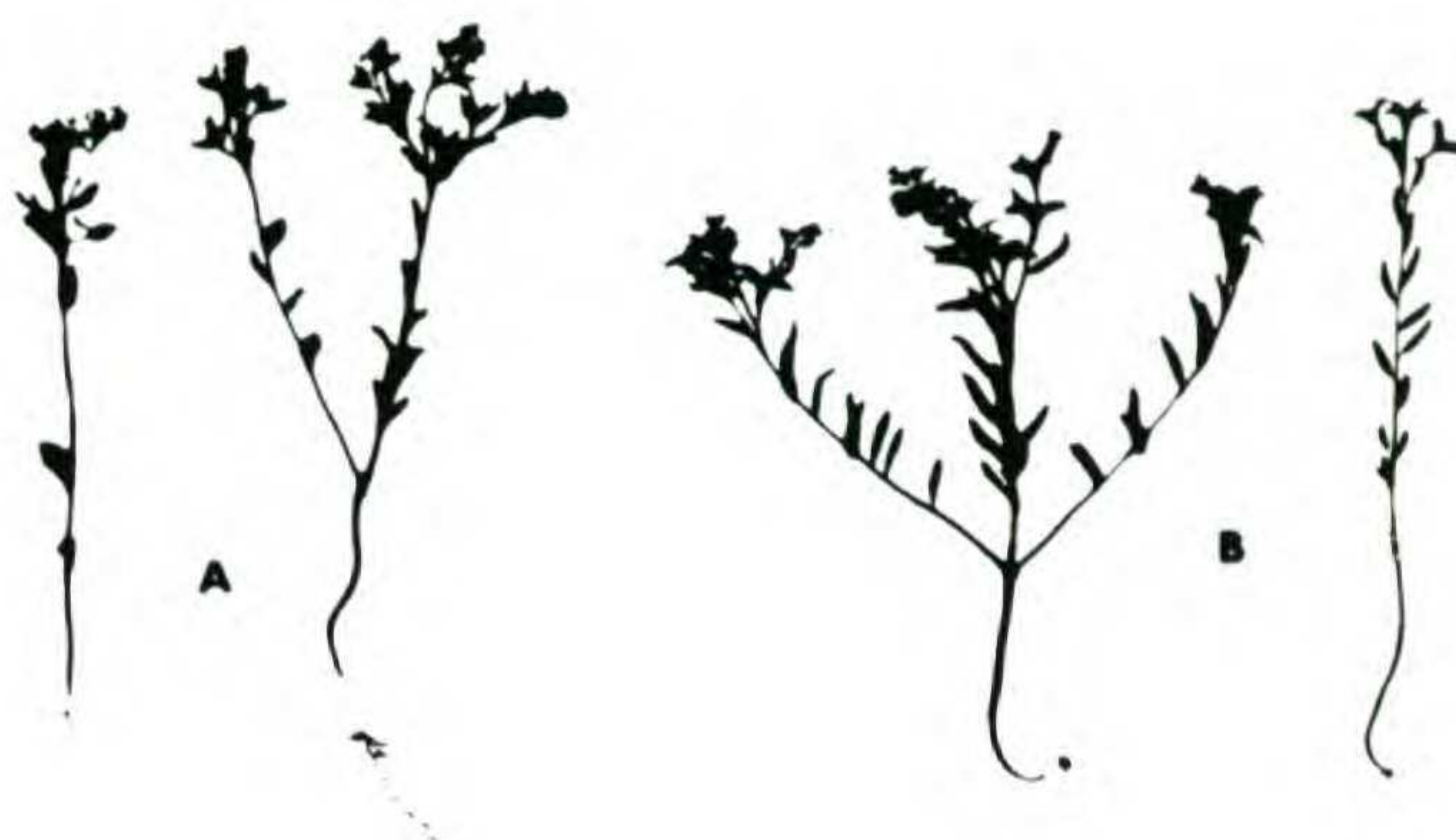
The tentative hypothesis is advanced that *P. dubia* is presently in the act of speciation and within recent times has produced an ecological race, *P. dubia* var. *georgiana*, at the southernmost boundary of its range and in adaptation to an ecological niche afforded by the granite outcrops. *P. maculata* may have had a similar origin in the past, but now exhibits the properties of a relict endemic because of its inability to compete successfully outside of a narrowly-restricted habitat which is gradually diminishing in extent.

SALTATIONAL SPECIATION

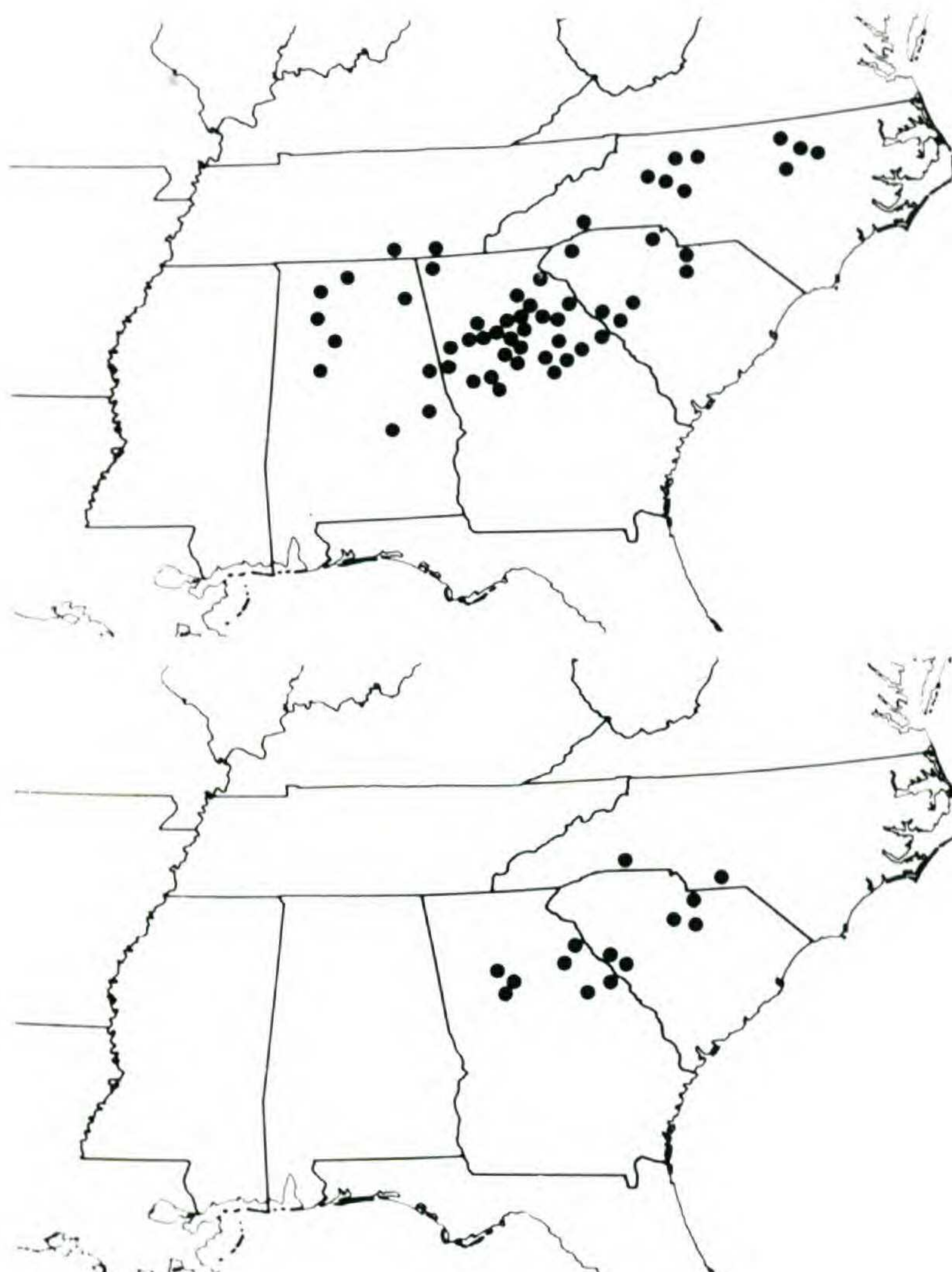
The occurrence of "species pairs" within outcrop communities, strikingly similar in life-form and ecology, but radically different in other important respects, suggests that saltational speciation may have been involved in their origin. The widely-fluctuating, outcrop environment would be a factor of significance in such a process. Three pairs of species will be discussed below: *Sedum pusillum* Michx. and *S. smallii* (Britt.) Ahles (*Diamorpha cymosa* (Nutt.) Britt.); *Talinum mengesii* Wolf and *T. teretifolium* Pursh; and *Cyperus granitophilus* McVaugh and *C. aristatus* Rottb. In none of these examples has a saltational mode of origin been clearly established. Instead, such a process is merely postulated on the basis of evidence presented below.

Sedum pusillum and *S. smallii*

Sedum pusillum is a small, succulent annual wholly confined to granite outcrop communities (Fig. 6, B + Fig. 8). It will grow in a variety of micro-habitats during "good" years, but is typically found growing in shallow, depression pits under the partial shade of pine or, more commonly, *Juniperus virginiana*. It is of systematic interest within the genus because of its low chromosome number, $2n = 8$ (Baldwin 1940), the lowest of any North American *Sedum*. It is of general evolutionary interest because of its endemism and remarkable similarity to *S. smallii* (Fig. 6, A). The latter is one of the most characteristic members of outcrop communities, but also occurs on sandstone outcrops



6



7

8

Fig. 6-8. Fig. 6. Habit of: A, *Sedum smallii* and B, *S. pusillum*.
Fig. 7, 8. Distribution maps. Fig. 7. *S. smallii*. Fig. 8. *S. pusillum*.

in Alabama, Tennessee, and Georgia (Fig. 7). It grows in abundance in the shallowest soils of depression pits where it has no competitors. Fröderström (1935), in his monograph on *Sedum*, considered the two species to be closely related. However, *S. smallii* has a very different chromosome number, $2n = 18$ (Baldwin 1940, O'Connell 1949, McCormick and Platt 1964).

Common base chromosome numbers in the Crassulaceae are 4 and 5, with most species being polyploid. The lowest numbers in each series are found in annuals (*Sedum pusillum*, $n = 4$, and *S. stellatum*, $n = 5$) within a family mostly composed of perennials. *Sedum smallii* is unusual in having a base chromosome number of 9 and Baldwin (1940) suggested that it may have originated as an amphidiploid. If this is taken as a working assumption, one of its parents could very well have been *S. pusillum*, the only extant member of the family with 4 pairs of chromosomes. Attempts should be made to produce interspecific hybrids which can be used for cytogenetic verification of the above hypothesis. For example, if 4 of the 9 chromosomes of *S. smallii* are homologous with the chromosomes of *S. pusillum*, 4 bivalents and 5 univalents should constitute the paired, meiotic condition in the hybrid. Positive results would warrant a search for the other parental species which should have 5 pairs of chromosomes.

Strong barriers to natural hybridization seem to be operative between the species. Populational analysis of a large outcrop in Rockdale County, Georgia, where both species are abundant, has yielded neither hybrids nor any indication of introgression. However, McCormick and Platt (1964) reported that: "Apparent intergeneric hybrids between *Sedum pusillum* \times *Diamorpha cymosa* were observed on one outcrop out of more than 100 visited". Several hundred artificial pollinations between the two species in the spring of 1967 failed to yield any seed, while control pollinations within each species resulted in a good yield.

Talinum engesii and *T. teretifolium*

The habit, habitat and distribution patterns of these two

Talinum species suggest that their separation into distinct, morphological entities might also have been brought about by a saltational process of speciation, which also involved polyploidy.

Talinum teretifolium ($2n = 48$) ranges from Pennsylvania to Georgia and grows in sandy or dry, rocky sites. In Georgia it is almost exclusively associated with granite exposures where it represents the only perennial in many of the shallow soils. *T. mengesii* ($2n = 24$) is found in western Georgia and it is the predominant species in Alabama, where it grows on the sandstone outcrops in Appalachian counties as well as on the granites of the Piedmont (Wolf 1939). Their ranges appear to have an allopatric pattern with a considerable overlap in Georgia. In the central Piedmont of Georgia, the predominant form is *T. teretifolium*, but pockets of *T. mengesii* populations have been located in the following Georgia counties: Douglas, Heard, Paulding, Rockdale, and Walton. Outcrops in the region of overlap support almost exclusively either one or the other species. At three sites in Georgia where plants of both species are contiguous, triploid hybrids have been found which are vigorous perennials, but apparently sterile.

The close morphological and distributional similarities between the two prompted Wolf (1939), in his evaluation of *Talinum* in Alabama, to postulate a common ancestry for them. Both species have a similar life-form and appear to occupy a very similar outcrop niche. Nevertheless, they are morphologically distinct species and can be readily separated on the basis of flower structure. *T. teretifolium* has small, rounded petals, fewer than 20 stamens, a short style, and flowers that open late in the afternoon, whereas *T. mengesii* has long, acute to mucronate petals, more than 40 stamens, a long, exserted style, and flowers that open early in the afternoon.

Plants of eighteen populations of *T. teretifolium*, from Georgia and South Carolina, were found to be tetraploid ($2n = 48$). Steiner (1944) gave similar counts for this

species but also reported a plant from Bibb Co., Alabama to be diploid ($2n = 24$). This is likely a case of misidentification since *T. teretifolium* has not otherwise been reported from this location which is in the heart of *T. mengesii* ($2n = 24$) territory.

It is suggested that the widespread, *Talinum teretifolium* is an amphidiploid species and that *T. mengesii* was one of its diploid progenitors. The proposed relationship for the *Talinum* species parallels that postulated for the *Sedum* species. In both pairs the polyploid member has a greater geographical range and is better adapted to exposed outcrop sites than its diploid partner, which in the case of *Sedum pusillum* is restricted to several granite outcrops in Georgia, South Carolina and North Carolina and in the case of *T. mengesii* is confined to the sandstone outcrops of Alabama and a few granite outcrops of Alabama and Georgia.

Cyperus granitophilus and *C. aristatus*

Cyperus granitophilus was first named by McVaugh in 1937 who considered it to be a form sufficiently distinct from the related *C. aristatus* (*C. inflexus*) to rank as a good species endemic to granite outcrop locations from North Carolina to Alabama. This classification was upheld by O'Neil (1942), in his taxonomic study of North and South American species of *Cyperus*, who added characters by which the two similar-looking sedges could be separated.

A recent systematic study (Wynne 1964) suggests that the endemic, *Cyperus granitophilus*, arose from the widely-distributed *C. aristatus* through autopolyploidy and subsequent selection for high ploidy levels in outcrop habitats. Data gathered from several natural populations and from herbarium specimens show the endemic to be distributed throughout the outcrop region (Fig. 5). It constitutes the predominant form in outcrop communities and grows in depression pits of little soil and scant competition. *C. aristatus*, on the other hand, is mostly found in border areas of deep soil where competition is more intense.

Plants of both species have been found to grow side by

side and both have more than once been mounted on the same herbarium sheet. Furthermore, character differences that separate them are almost all quantitative. When compared on the basis of spikelet, scale, and achene dimensions, the endemic is larger in every respect. Chromosome counts showed high, but variable, numbers within populations and *C. granitophilus* had a consistently higher chromosome number ($2n = \text{ca. } 80, 88, 96$) than *C. aristatus* ($2n = \text{ca. } 48, 56, 64$).

Many interesting questions have been raised by this preliminary study. One of the most widespread effects of polyploidy is to increase the water content of the cell relative to the amount of protoplasm, which in turn is believed to be a result of increase in cell size (Noggle 1949, Stebbins 1950). Could this provide increased drought resistance necessary for *C. granitophilus* to become the prevailing form in xeric, outcrop habitats? Furthermore, does this example represent a mechanism whereby a monotypic, widespread species, itself probably polyploid, could produce an ecotype able to exploit an available, but marginal, habitat by further increase in the ploidy level? Further experimental work is needed before definite answers can be given to the above questions.

CONCLUSION

The granite outcrop region constitutes an area of high endemic frequency in the southeast and the greatest number of endemic taxa occur in the central Piedmont of Georgia. Several different types of endemics are represented in outcrop communities including at least one monotypic genus, endemic species with and without related species nearby, and infraspecific taxa which appear to be ecotypes of extant species. The implication derived from this array of endemic types is that the granite outcrops have served as active sites for plant speciation for a long period of time.

The scattered distribution of rock exposures increases the probability that their populations will diverge from one another with time. An ideal situation for ecogeographical

speciation is established when such unusual and disjunct habitats are located at the boundary of a species range. Semi-isolated, geographically-peripheral populations are afforded an ecologically-marginal habitat to which they may adapt. Subsequent migration, immigration and genetical interaction among such populations could eventually produce an endemic ecotype, which, in time, could ultimately become an endemic species. This appears to be the manner by which the ecotype *Phacelia dubia* var. *georgiana* originated in the recent past from the Appalachian *P. dubia*, and may, in turn, closely parallel the manner by which the endemic *P. maculata* originated from an Appalachian progenitor in the remote past. Species which also appear to have had a gradual, ecogeographical origin, but from Coastal Plain progenitors, include *Portulaca smallii* and *Rhynchospora saxicola*.

The disjunct distribution of outcrop communities, together with their variable size and extreme environmental conditions, might all be factors contributing to the saltational origin of various taxa. Drastic fluctuations in population size could on the one hand lead to local extinction (endemic species may be totally lacking at one outcrop and abundant at another outcrop a few miles away), but could also be conducive to "catastrophic selection" (Lewis 1966), whereby a few individuals, possessing favorable genotypes, would be the sole survivors at a particular outcrop site and provide progeny for repopulation.

Three sympatric "species pairs," similar (but not identical) in vegetative morphology and in ecological adaptation, but different in other important respects, are presented as possible cases of saltational speciation. *Sedum smallii* ($2n = 18$) may have originated through allopolyploidy involving the rare endemic *S. pusillum* ($2n = 8$) as one parental species and an unknown, 5-chromosome species as the other parent. *Cyperus granitophilus* may be an autopolyploid form of *C. aristatus* and appears to be better adapted to outcrop habitats than the latter. Finally, *T. teret trifolium* ($2n = 48$) may have originated as an amphidiploid with

T. mengesii ($2n = 24$) as one of its parental species. In all three examples, the polyploid member of each pair is more widely distributed than its diploid, or, in the case of *Cyperus*, its lower polyploid relative.

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